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Leaf Fall and Litter Disappearance in a Tropical Forest

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With 5 figures in the text

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1. Introduction

The interest in the role of soil fauna in decomposing leaf litter and subsequently incorporating it into the soil has recently increased. In temperate regions, it is known that certain groups of soil animals are important agents in fragmenting or burying fallen litter. Thus, millipedes (Bocock, 1963), and also tipulid (Priesner, 1961) and bibionid larvae (d'Aguilar and Bessard, 1963) skeletonize leaf tissues, while lumbricids bury fallen leaves (Raw, 1962; Edwards and Heath, 1963). Smaller arthropods, such as soil mites and Collembola (Shanks and Olson, 1961; Crossley and Hoglund, 1962; Edwards and Heath, 1963; Zachariae 1963) erode leaf surfaces or tunnel into them.

There are two main objects to this work. First, to investigate the seasonal sequence of leaf-fall and rate of litter disappearance; secondly, to investigate the activity of the soil and litter fauna on the disappearance of different species of fallen leaves in relation to climate. No references to such work in tropical forests can be found.

2. Description of the site

The site, of approximately one acre, is situated in the Botanic Garden of the University of Ibadan, Nigeria. Its early history is unknown but it was possibly once under shifting cultivation; it has remained undisturbed for at least 15 years. The natural vegetation lies on the border of the mixed, dry lowland forest zone (Keay, 1953), at approximately 250 meters altitude, with a mean annual rainfall of about 120 cm. and a mean annual temperature range of 21—32 °C.

The rainy season generally lasts from May to September and the dry from November to March; intermediate months have a sporadic but heavy rainfall.

An area, 15×15 meters, was marked out in the forest and the natural vegetation identified. Woody species dominate in a more or less closed canopy; there is a sparse shrub layer but no field or ground layers. The most common species of the upper storey are *Alchornea cordifolia*, *Alstonia congensis*, *Bosquei angolensis* and *Sterculia tragacantha*. Other species include *Ficus* sp., *Trichilia heudelotti*, *Theobroma cacao* and *Palmae* sp. (palm). The lower storey includes *Funtumia africana*, *Mallotus subulotus* and *Pycanthus angolensis*. The shrub layer consists of *Celtis* sp., *Dracaena* sp., *Napoleona vogeli* and saplings of *Bosquei* sp., *Mallotus* sp., *Trichilia* sp. and *Rubus* sp.

The forest floor slopes gradually to a stream, and may become partly flooded for short periods during the rainy season. The ground is covered by a thin layer of litter, but patches of soil are exposed during the wet season. A thick layer of earthworm casts is then produced, but during the dry season and at the start of the following wet season these disintegrate or are washed away, to be replaced by new casts. The soil profile (pH 5.3—7.4) consists of a superficial cover of earthworm casts and a humic, loamy fine sand layer, followed by a uniform, loamy layer 2—5 cm. deep (the "earthworm horizon"). This is followed by a reddish-brown, loamy coarse sand, with roots and a few stones, of unknown depth, below.

3. Leaf-fall

3.1. Experimental methods

Leaf-fall was collected at fortnightly intervals during $13^1/_2$ months (late Feb. 1963 — early April 1964) in six leaf traps with a wooden frame (1×1×0.7 m.) and a wire mesh floor, 0.2 m. above the ground. The litter was air-dried at 26 °C ± 3 °C and 45—55% R. H., and the leaves then identified and counted. The leaves were separated from the litter debris, i. e. fallen twigs, seeds, flower-heads etc. and weighed separately. Exceptionally heavy rainfall and extensive flooding during late August and early September 1963 interrupted the experiments for several weeks.

Litter on the forest floor was also collected periodically from six quadrats, 1×1 m., air-dried in the laboratory and then weighed. Maximum and minimum temperatures 1.5 m. above the ground were taken every 2 weeks and periodically compared with temperatures within the litter. Rainfall measurements and windspeeds were obtained from the University Meteorological Station nearby.

3.2. Experimental results

3.2.1. *Annual leaf-fall*

Fig. 1 shows the total amount of leaf-fall during 13 ½ months, collected at fortnightly intervals, including daily rainfall and 14-day maximum-minimum temperatures (differences between air and litter temperatures were usually insignificant). Fluctuations in leaf-fall during the wet season are generally low and insignificant. At the start of the dry season it progressively increases, culminating in a pronounced peak during the driest period, and then falling off again. Leaf-fall is over 10 times greater during the driest month compared with the wettest. Average temperature fluctuations are usually greatest during the dry months and least during the wet; hence, leaf-fall may also be related to temperature.

No effect was detectable between wind (km. run per week) and the weights of leaf-fall and litter debris (fig. 2). However, early 1963 had irregular, but strong, gusts of wind, which probably accounted for relatively large falls of litter debris during that time. Also, there was a longer dry season during early 1963 compared with later that year and early 1964, resulting in more dead wood.

Fig. 3 shows the culminative totals of leaf-fall of seven species of trees studied. These species accounted for half the number identified, but made up the bulk of the total number of leaves collected (91%; 6% others; 3% unidentified). The annual patterns of leaf-fall of the seven species are summarised as follows.

Bosquei angolensis shed few leaves during wet months compared with dry months; leaf-fall progressively increases to a peak in the middle of the dry season, and then declines.

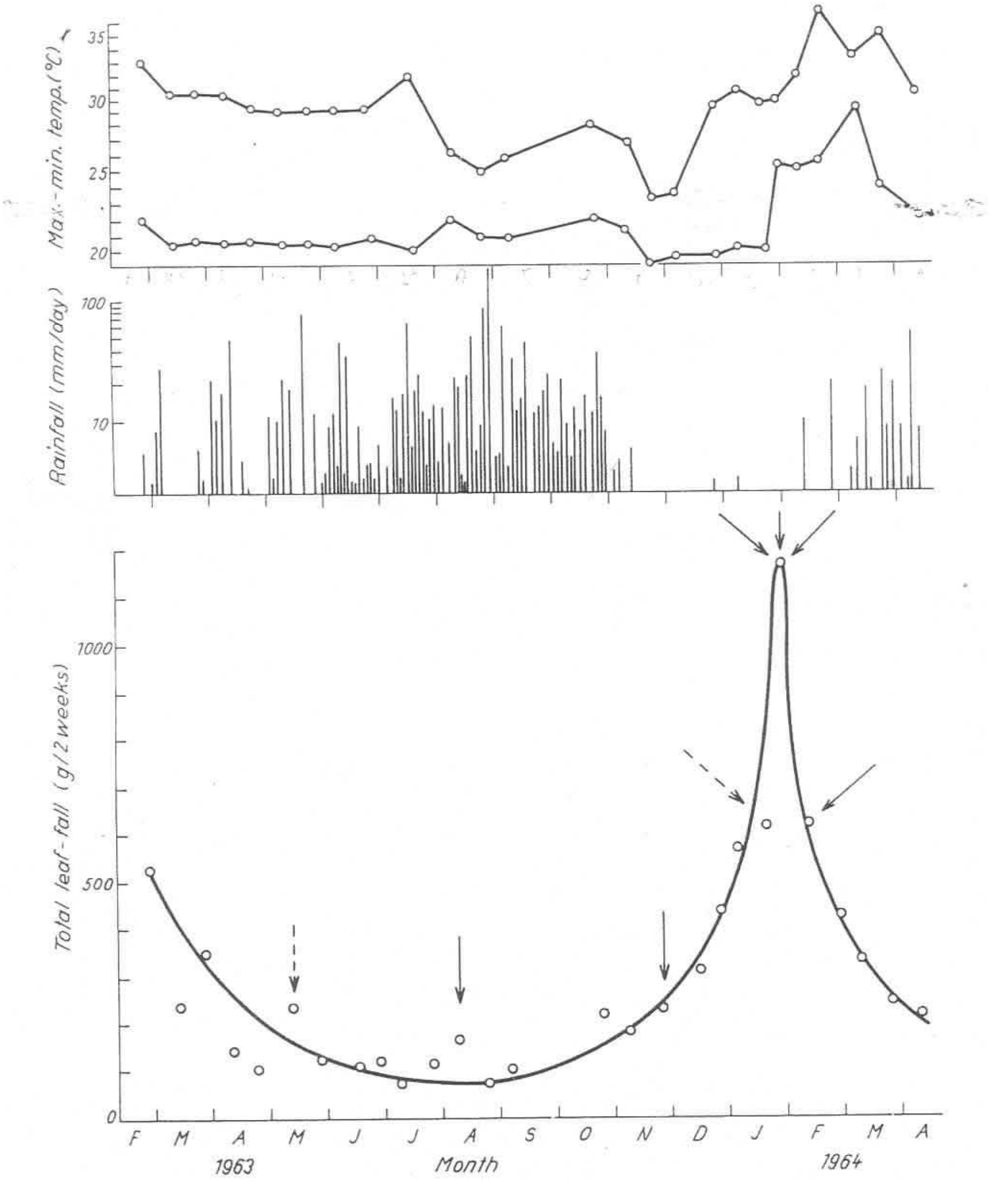

Fig. 1. Seasonal leaf-fall in a tropical forest at Ibadan, Nigeria. Arrows indicate maximum leaf-shedding for seven tree species.

Sterculia tragacantha first shed leaves early in the dry season, reaching a maximum in early December, and then declined and remained steady from March onwards, but there was a minor peak at the end of May.

Alstonia congensis showed two periods of leaf-fall, one in mid January and another, less heavy, in mid May, i. e. in the middle of the dry season and at the start of the wet. Most leaves were shed during two weeks on both occasions.

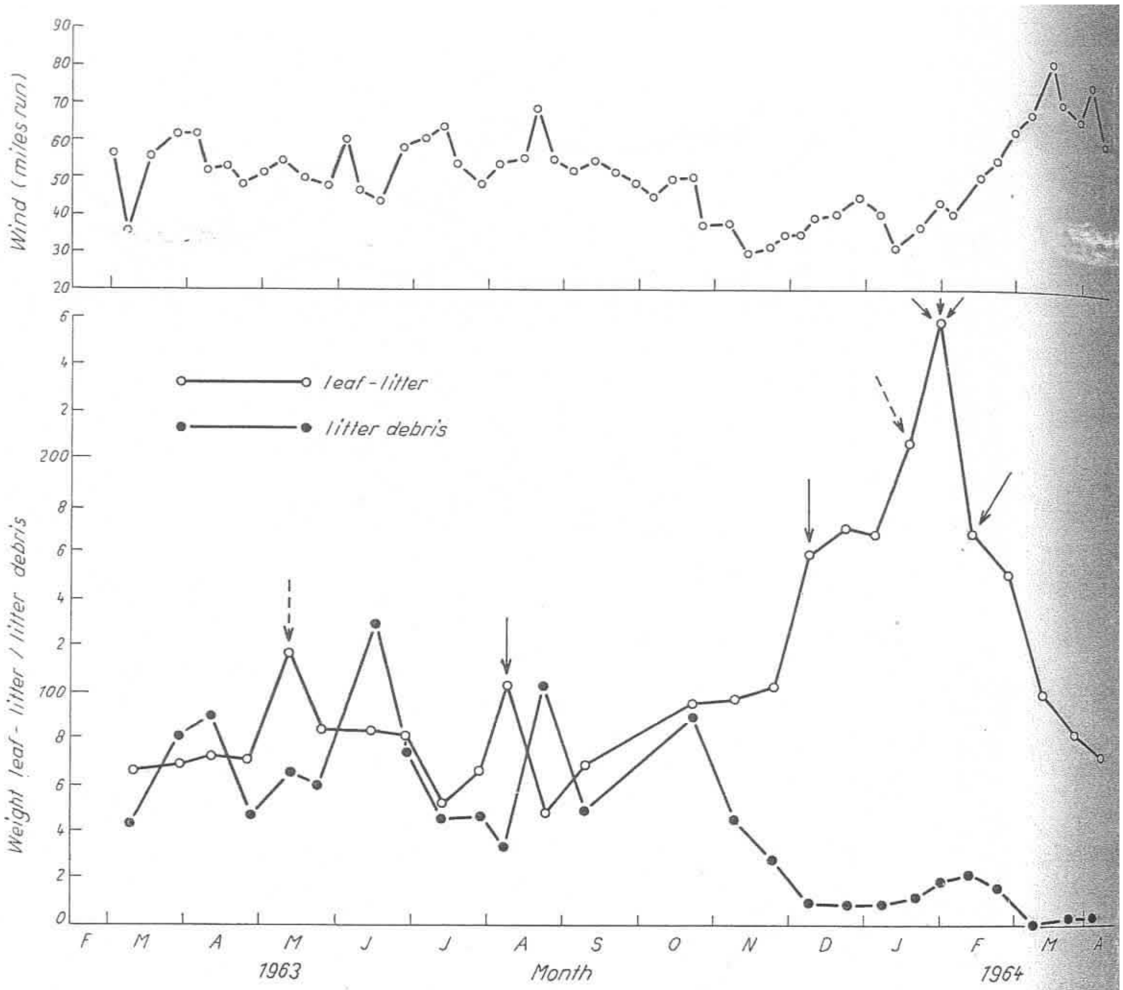

Fig. 2. Average weight (g/m²) of leaf-litter and litter debris, collected at fortnightly intervals, at Ibadan, compared with wind (km. run per week). Arrows indicate maximum leaf-shedding for seven tree species.
Note. — For: Wind (miles run), read: Wind (km. run).

Trichilia heudelotti shed leaves gradually from the start of the dry season; most fell in mid-February and fewer fell from mid-March throughout the wet season.

Funtumia africana shed most of its leaves at the same time as *Bosquei*. Few leaves fell during the remainder of the year.

Theobroma cacao shed its leaves mainly from the end of January to mid March.

Alchornea cordifolia was the only species to shed its leaves during the middle of the wet season, although some fell at the start and end of the dry season. Observations during the second wet season confirmed this, although total leaf-fall was less.

There is therefore a well-defined sequential pattern of leaf-fall from the different trees studied. This activity is generally maintained throughout the dry season, showing different maxima in December and January and, with one exception (*Alstonia*), showing low, minor fluctuations during the remainder of the year. Leaf-shedding in one species (*Alchornea*) was observed only during the wet season.

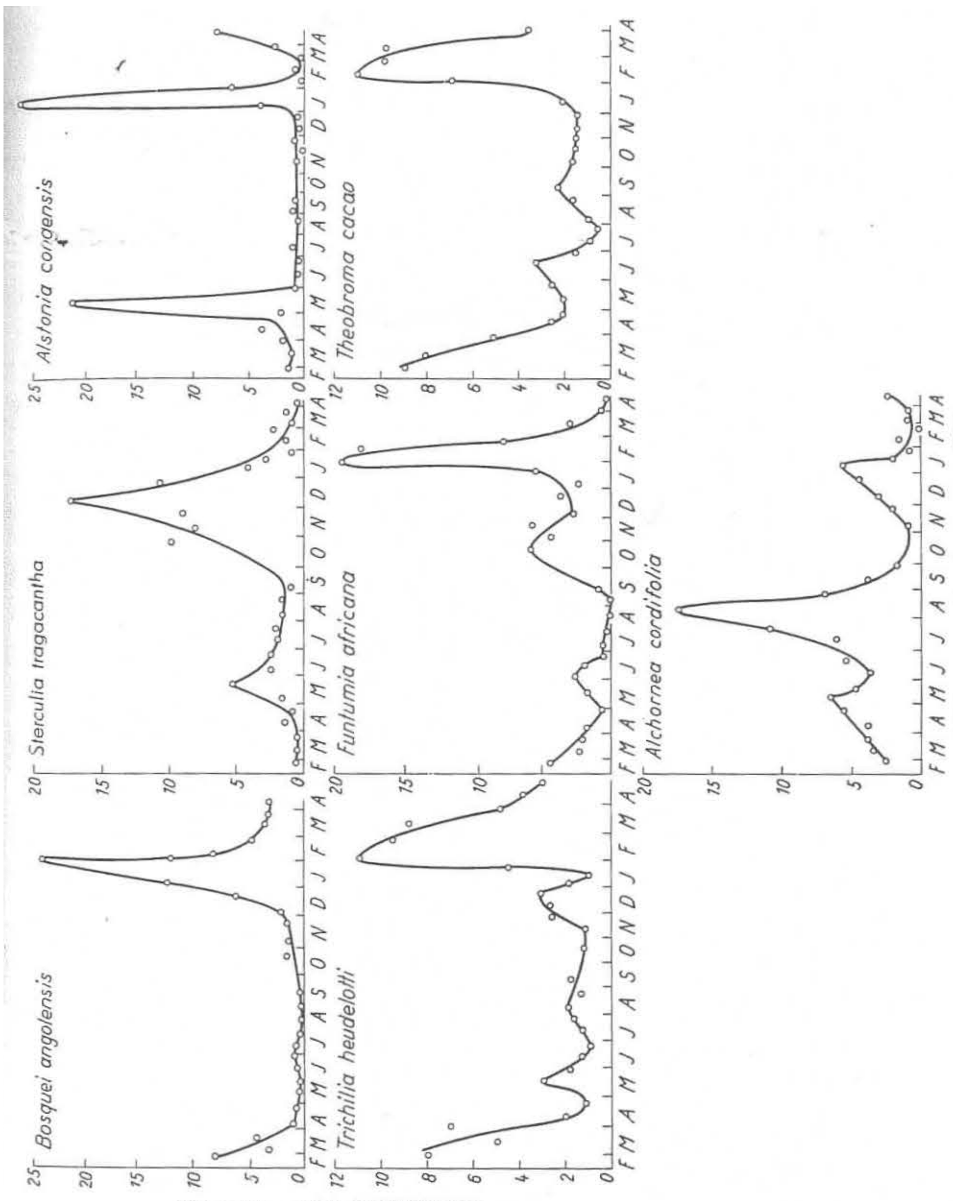

Fig. 3. Seasonal leaf-fall for seven tree species in a forest at Ibadan.

3.2.2. *Rate of litter disappearance*

The total amount of litter in the forest at Ibadan was over 5,600 kg./hectare per annum (dry matter), of which leaves formed about 2/3 of the total, the remainder being debris. This total is appreciably less than that found by LAUDELOUT and MEYER (1954) in the Belgian Congo, with 12,300 kg./hectare per annum (range 11,000—13,700 kg./hectare), NYE (1961) in Ghana, with 9,400 kg. oven dry matter/hectare, JENNY et al (1949) in Colombia, with 7,600—10,700 kg. dry matter/hectare and WEBB (1956) in Australia, with 5,600 kg. oven dry matter (leaves only)/hectare.

The litter on the ground averaged 2,450 kg./hectare (range 2,230—3,170 kg./hectare) during the dry months and 1,700 kg./hectare (range 1,150—2,580 kg./hectare) during the wet. The annual rate of litter decomposition, calculated from Nye's (1961) method (according to which the annual rate of litter turnover is expressed as a proportion of that lying on the soil surface at any one time), varied from 200 % (end of January) to 485 % (end of July). These figures compare with a litter decomposition rate of 316 % per year for forests in the Belgian Congo (Laudelout and Meyer, 1954; Nye, 1961) and 465 % per year for forests in Ghana (Nye, 1961). These results are based on regions with differing seasonal leaf-fall, so comparisons are probably unreliable.

4. Litter disappearance

4.1. Experimental methods

Leaf-discs, 2.5 cm. in diameter, belonging to 5 different tree species, *Bosquei angolensis, Sterculia tragacantha, Trichilia heudelotti, Alchornea cordifolia* and *Theobroma cacao*, were obtained from freshly fallen leaves and 20 discs of each species were laid evenly in separate terylene bags (16 cm. × 20 cm.) of meshes 0.002 mm., 1.25 mm., 2.50 mm. and 10.00 mm. The bags were firmly pegged on to the bare forest soil surface and soon became buried under falling leaves. Four sets of 4 bags with different meshes were used for each species. One set was collected every 10—20 days and then replaced, so that each set was left undisturbed on the ground for 6—12 weeks.

When collected, the litter bags were placed in polythene bags and taken to the laboratory where the fauna were immediately extracted from the leaf-discs by Tullgren funnels. The leaf-area eaten by the fauna was then visually estimated by placing the discs in between two glass sheets over a 0.5 sq. cm. grid. The discs were then replaced in the bags which were again pegged at random on the forest floor and the procedure repeated at intervals until the discs had disappeared. This method of estimating leaf-disappearance involves maximal errors of about 10%; Heath, Edwards and Arnold (1964) found a close correlation between this method and a photoelectric method.

In further experiments, known numbers of leaves in open wooden cages with a wire mesh top were left on the soil surface (Raw, 1962). Occasional inspection showed that the rate of litter decomposition in the cages was a fifth to a tenth faster than in the bags.

The experiments were started towards the end of the wet season, continued throughout the dry season and ended during the following wet season. They were again repeated during the wet season, and lasted under 2 months, by which time all the leaf tissue had gone.

4.2. Experimental results

4.2.1. *Activity of microarthropods*

Table 1 gives the litter fauna population during the wet season, showing that the dominant groups numerically were mites and Collembola (53 % and 34 % respectively). The total fauna — 38 thousand per square meter — is fairly low compared with some results in temperate regions (e. g. Murphy, 1953), and there were remarkably few termites, which are usually abundant in forest litter in the tropics (Maldague, 1961). The litter was also sampled during the dry season, when only a total of about 400 soil animals were recovered per square meter.

Fig. 4 gives the rate of disappearance of the leaf-discs in relation to the total number of microarthropods per sample at various intervals from the end of one wet season until the start of the next. By the end of the experiment, all the leaf-tissue had been skeletonized, leaving only the midribs and a fine broken meshwork of small leaf veins.

The results are summarised as follows.

(1) Over 90 % of the leaf-discs remained untouched in the litter bags with the finest mesh. A few small Collembola and mites found in these bags made up less than 2 % of the total number of litter fauna recovered from the larger mesh bags. The distribution of the different kinds of soil fauna in the other bags was about the same, although a few large millipedes and woodlice were found in the largest mesh bags and not in the others; ants and termites were missing in the bags with the smaller meshes (0.002 mm. and

Table 1 Population of litter fauna in numbers per sq. meter during the wet season (May 1964) (average of 36 samples, 7 cm. diameter)

ARACHNIDA			COLLEMBOLA		INSECTA		MYRIAPODA	
Trombidiformes	540		Onychiuridae	2,760	Coleoptera	260	Diplopoda (juv.)	1,210
Mesostigmata (Parasitidae)	1,190		Poduridae	1,300	Diptera	1,540	Chilopoda	30
			Isotomidae	4,130	Hymenoptera (Formicidae)	870	Symphyla	15
								1,255
Mesostigmata (Rhodacaridae)	260		Entomobryidae	4,290	Lepidoptera	45	OTHER ARTHROPODA	
			Sminthuridae	415	Thysanoptera	30	Isopoda	415
Uropodina	430							
Oribatidae	17,330			12,895	Hemiptera	40	OTHER FAUNA	
	19,750							
Araneae	130				Isoptera	30	Oligochaeta	34
Opiliones	40	20,350			Protura	15	Enchytraeidae	190
Pseudoscorpions	430				Diplura	70	Nematoda	760
	600					2,900		
			33,245		15,795			
					37,815			

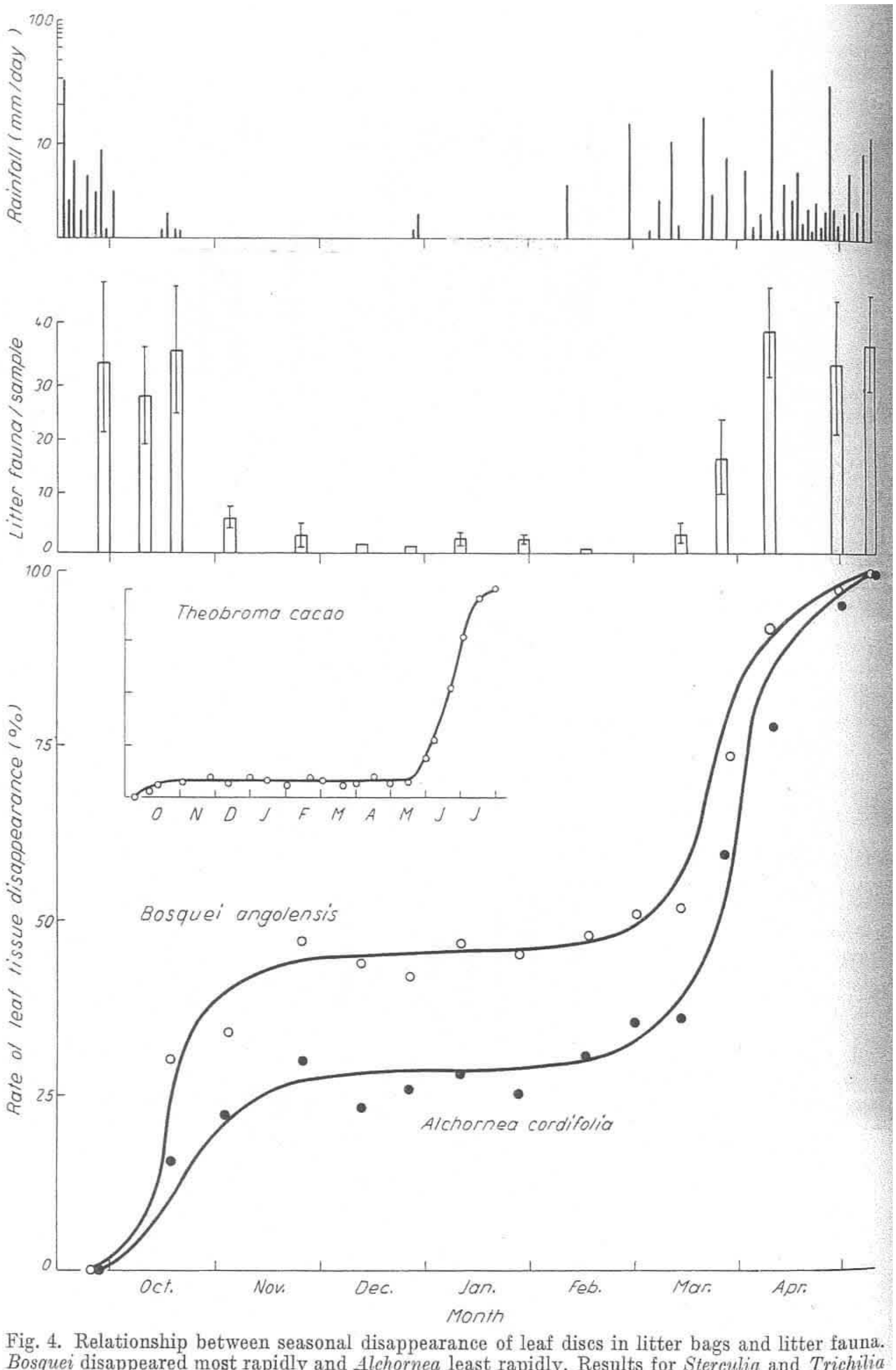

Fig. 4. Relationship between seasonal disappearance of leaf discs in litter bags and litter fauna. *Bosquei* disappeared most rapidly and *Alchornea* least rapidly. Results for *Sterculia* and *Trichilia* (not shown) intermediate.

1.25 mm.). Except for the smallest mesh bags, the rates of litter disappearance in the other bags were approximately similar, showing that the fewer, larger, arthropods in these bags did not substantially affect the rate of litter disappearance (table 2).

Table 2 Average fauna in litter bags of different meshes during the wet (above) and dry season (below)

Fauna	Mesh bags (m.m.)			
	0.002	1.25	2.50	10.00
Oribatoidea	0.3	16 ± 4.2	16 ± 3.9	18 ± 4.9
Other Arachnida	—	14 ± 3.7	12 ± 4.0	4 ± 1.1
Collembola	0.3	1.1	2.3	2.1
Other Insecta	—	—	0.3	0.2
Myriapoda	—	—	0.1	0.4
Rest	—	—	—	—
Oribatoidea	—	0.5	0.6	1.4
Other Arachnida	—	—	—	—
Collembola	—	0.3	0.8	0.3
Other Insecta	—	—	—	—
Myriapoda	—	—	—	0.1
Rest	—	—	—	—

(2) There were many more animals on the leaf discs during the wet season than the dry (fig. 4), showing a clear parallel between the number of soil fauna and the rate of disappearance of the discs. Between 25—45 % of the discs were eaten during the first 4 weeks, i. e. by the end of the first wet season. Fragmentation almost ceased during the 5 months of the dry season, when only 2—6 % of the leaf tissue disappeared. During the following wet season the rate of leaf disappearance rapidly accelerated, the remaining tissues being eaten in about 5 weeks.

(3) The leaf discs of the different tree species disappeared at different rates, *Bosquei* most rapidly, followed by *Sterculia*, *Trichilia* and *Alchornea*, the rate of disappearance of the first being approximately twice that of the last. Leaf discs of *Theobroma* disappeared at a much slower rate, remaining little affected by the end of the first wet period and during the dry season, when about 10 % of the tissues were eaten (fig. 4). During the following wet season, however, the leaves gradually disappeared over 2 ½ months. Numbers of soil animals found in these bags were slightly lower than in the others.

Experiments on the rate of disappearance of leaf discs of *Bosquei* and *Alchornea* by the soil fauna were repeated during the following wet season. The results, given in fig. 5, showed that the rate of litter disappearance was very rapid; it was completed in 4 weeks for *Bosquei* and in 6 weeks for *Alchornea*. There was little indication of faunal activity for the first 10 days, then the leaf discs were rapidly eaten and none remained 3—4 weeks later.

4.2.2. *Activity of earthworms*

A feature of the forest floor in Nigeria is the presence of numerous vertical earthworm casts, 3—8 cm. high and 1—3 cm. in diameter, produced by the earthworm *Hyperiodrilus africanus* (BEDDARD). Such casts are illustrated in NYE, 1954 and BATES, 1960. Casting activity is limited to the wet season. During the dry season and at the start of the following wet season, the casts disintegrate to a fine, sandy loam, forming the CrW horizon, as described by NYE (1954).

4.2.2.1. Estimation of earthworm population

Estimations were made during the second month of the wet season, using RAW's (1959) diluted formalin method, 25 ml. of 40 % formalin being added to 1 gal. of water and this

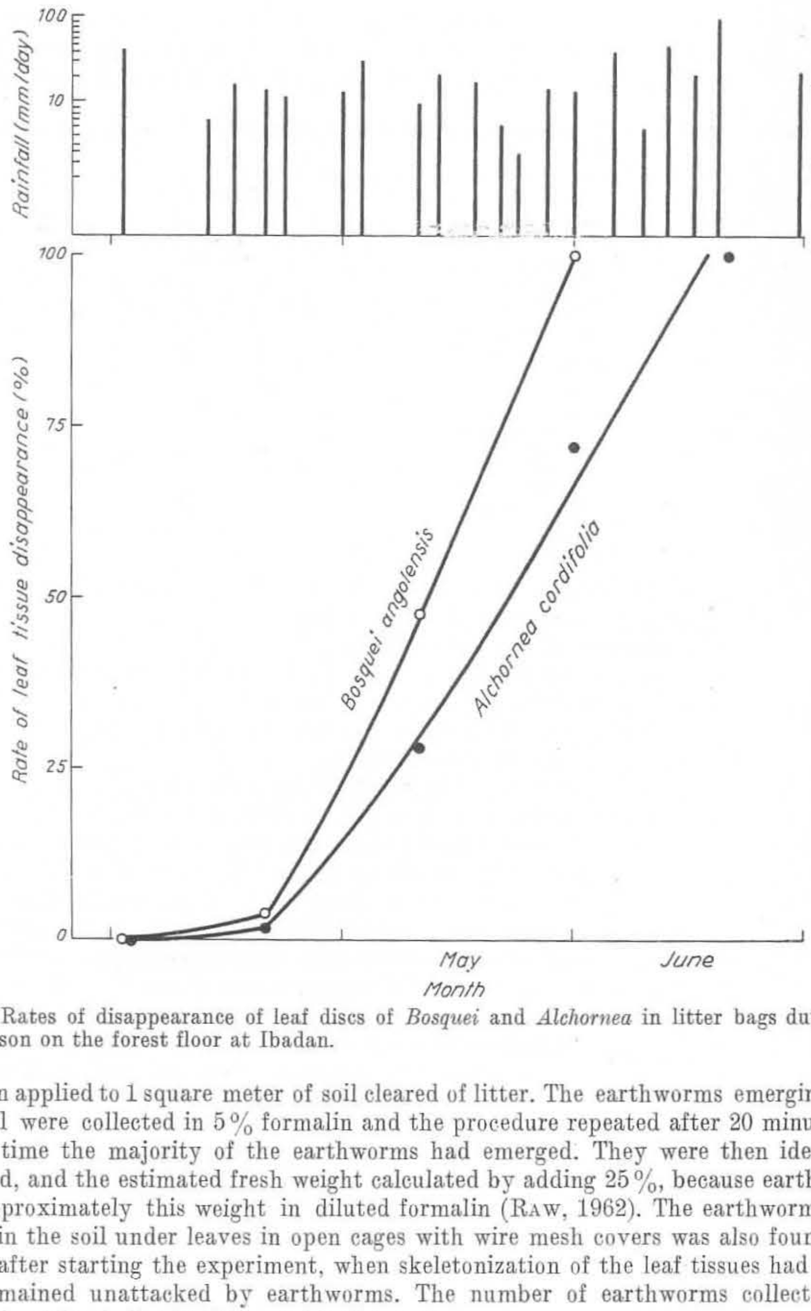

Fig. 5. Rates of disappearance of leaf discs of *Bosquei* and *Alchornea* in litter bags during the wet season on the forest floor at Ibadan.

solution applied to 1 square meter of soil cleared of litter. The earthworms emerging from the soil were collected in 5% formalin and the procedure repeated after 20 minutes, by which time the majority of the earthworms had emerged. They were then identified, weighed, and the estimated fresh weight calculated by adding 25%, because earthworms lose approximately this weight in diluted formalin (RAW, 1962). The earthworm population in the soil under leaves in open cages with wire mesh covers was also found 3—4 weeks after starting the experiment, when skeletonization of the leaf tissues had begun, but remained unattacked by earthworms. The number of earthworms collected was approximately similar to that outside the cages.

Table 3 gives the average number and weight of earthworms per square meter. There were about 140,000 earthworms (per acre 57,000 per ha.), weighing 40.5 kg./acre (16.4 kg./ha.). These results are generally lower than those obtained from grassland in temperate regions (EVANS, 1948).

Table 3 Earthworm population in forest soil during the wet season (May, 1964) at Ibadan. Average of 6 quadrats, 1 sq. meter each

Size range (cm.)	Estimated fresh weight (gm./sq. meter)	Numbers (/sq. meter)
18—12	4.4	1.7
11— 8	2.3	3.7
7— 4	1.9	7.8
< 4	1.6	21.0
Total	10.2	34.2

4.2.2.2. Weight of earthworm casts

Earthworm casts were collected from five quadrats, each 1 meter square, at 2-monthly intervals for 12 months, oven-dried at 105 °C for 2—3 days and then weighed (table 4). New casts were only produced during the wet season, the old casts slowly disintegrating during the dry season and more rapidly at the start of the following wet season, when casting was once more resumed. About 90 tons/acre (36.4 tonnes/ha.) /12 months of (new) casts were produced, which is over 8 times more than is produced by lumbricids in temperate regions (EVANS, 1948), but is slightly less than NYE (1954) found in Ghana.

Table 4 Weight of earthworm casts (gm./sq. meter) in forest soil at Ibadan (mean of 5 quadrats, 1 sq. meter each)

MONTH	Oct.	Dec.	Feb.	April	June	Aug.
Average weight*) (mg./sq. meter)	2,050 old	1,400 old	1,950 old	500 old 1,760 new	2,100 new — old	2,400 new
Standard deviation	± 397	± 98	± 91	± 79 ± 127	± 304	± 362

*) rounded off to the nearest 50 gms.

4.2.2.3. Earthworm activity and litter disappearance

The effect of earthworms on litter was estimated by placing known numbers of freshly fallen leaves inside wooden cages on the soil and periodically inspecting the leaves (RAW, 1962). Each cage consisted of a wooden frame (100 × 100 × 10 cm.) pegged to the ground and covered on top by 1 cm. mesh wire. Five cages, with a mixed collection of 5 different tree species of leaves were laid out at random towards the end of the wet season and examined at fortnightly intervals, when they were counted, until the following wet season, when the experiment was repeated.

During the first wet season the activity of microarthropods skeletonized more than one-third of the total leaf material. The leaves remained untouched during the dry season, but at the onset and during the first month of the next wet season, the leaf tissue rapidly disappeared, leaving only the midribs. During the wet period, numerous earthworm casts became pushed in between the leaves and in between broken remains of leaf tissue, but there was never any evidence of leaf-burial by the earthworms. Furthermore, when earthworm burrows were carefully examined, they showed no trace of leaf fragments. Hence, *Hyperiodrilus africanus* appears to play no part in burying fallen leaves, unlike lumbricids in temperate regions. However, casts produced during the wet season eventually fell and disintegrated, covering the leaves soon after the start of the following wet season. Thus, these earthworms indirectly contributed in burying the remaining leaf

Table 5 Litter-fall and litter accumulation in

PLACE	VEGETATION	RAINFALL (cm./yr.)	TEMPERATURE (°C; average/yr.)
TROPICAL REGIONS			
Calima, Colombia	Broad-leaved rain forest	825	25.5
Chinchina, Colombia	Broad-leaved forest	255	21
Yangambi, Belgian Congo	Mixed rain forest	170	24.5
Kade, Ghana	Moist semi-decidous-moist evergreen forest	163	18
Ibadan, Nigeria	Mixed dry lowland forest	120	27
TEMPERATE REGIONS			
California, U.S.A.	Oak woodland	75	10
California, U.S.A.	Pine stand	75	10
Holland	Mixed woodland	85	10

fragments. The newer and smaller casts produced at the start of the wet season remained intact, and frequently became intermingled with broken fragments of leaf debris.

5. General discussion

5.1. Leaf-fall and litter disappearance

Leaf-fall in a tropical forest may be continuous (NYE, 1961) or seasonal (JENNY et al, 1949; LAUDELOUT and MEYER, 1954). Unlike temperate forests, even when seasonal, some leaves fall continuously throughout the year, but mainly during the dry season. Thus, at Ibadan, the rate of leaf-fall during the middle of the dry period is over 10 times greater than the remainder of the year. Furthermore, different trees shed leaves at different intervals during the dry season, giving a marked sequential pattern to leaf-fall.

Table 5 compares the results of various workers, and shows little relationship between leaf-fall, rate of litter accumulation and the average temperature and rainfall in different regions. Generally, in tropical forests, there is little or no litter accumulation and this results in a fast turnover of organic matter in the soil. In temperate forests, litter accumulates; the equilibrium between leaf-fall and litter accumulation may take many years, as for instance, in coniferous stands in temperate regions.

NYE (1961) in Ghana and LAUDELOUT and MEYER (1954) in the Belgian Congo found that the ground litter disappeared at the rate of 1.3% and 0.9% per day respectively. At Ibadan, this varies between 0.6% per day during the dry season and 1.5% per day during the wet. Under these conditions, 95% equilibrium of the forest floor in Ghana, the Belgian Congo and at Ibadan will be reached in 2—3 years. In tropical forests in Colombia (JENNY et al, 1949) it will be attained in 3—6 years, in temperate oak woodlands in California 25—50 years, and in pine stands in California 100—300 years (JENNY et al, 1949). BRAY (1964) has recently published extensive data for litter production of forests in many regions.

various regions and at Ibadan in relation to rainfall and temperature

A. LITTER FALL (kg./hectare/yr.)	B. LITTER ACCUMULATION (Kg./hectare)	RATIO A : B	AUTHORITY
7,560	4,500	1.7 : 1	Jenny et. al., 1949; Jenny, 1948
9,000	14,700	1 : 1.6	Jenny et. al., 1949; Jenny, 1948
12,300	4,300 (estimated)	2.9 : 1	Bernard, 1945; Landelout & Meyer, 1954
9,400	2,220	4.2 : 1	Greenland & Kowal, 1960; Nye, 1961
5,600	1,700—2,450	2.2 : 1	Present work
1,380	39,980	1 : 29.0	Jenny et. al., 1949
2,800	167,700	1 : 59.6	Jenny et. al., 1949
3,100	3,600	1 : 1.2	Witkamp & van der Drift, 1961

Generally, more litter falls in tropical forests than in temperate ones, but this is not invariably so. In tropical forests litter-fall varies from 5,600 to over 12,000 kg. per hectare per year. In temperate forests, the average litter-fall in birch and spruce stands in Scandinavia varies from about 1,900—3,400 kg. per hectare per year (Handley, 1954; from various authors); in pine stands in California 800—3,000 kg. (Jenny et al, 1949); in mixed oak-birch stands in Holland 3,100 kg. (Witkamp and van der Drift, 1961) and in mixed oak and beech stands in England 2,600—3,000 kg. per hectare per year (Heath, 1961). Pearsall (1945) estimated an annual litter-fall of over 16,000 kg. per hectare in an oak woodland in Hertfordshire, England, which is probably the highest yet recorded.

5.2. Influence of microarthropods on litter disappearance

In temperate regions, the relative importance of microarthropods in breakdown of leaf tissues has been assessed by exposing leaf discs in mesh bags, and either weighing or measuring the area of the discs at intervals. Shanks and Olson (1961) and Edwards and Heath (1963) found that about ½ and ¾ of exposed areas of leaf discs respectively disappeared from a woodland floor in a year. Crossley and Hoglund (1962) found a good correlation between the number of microarthropods in litter bags and the rate of litter disappearance. During winter there were fewer animals on the leaf discs and less leaf tissue was eaten, compared with the summer, when more was eaten by more animals. Crossley and Hoglund (1962) also found that the number of arthropods in the litter depended on the moisture content of the litter. Edwards and Heath (1963) observed that after heavy rain leaf discs disappeared more rapidly than in dry periods, and van der Drift (1963) suggested that moisture was more important than temperature in litter decay.

No work appears to have been done on the relation between litter disappearance and litter fauna in tropical forests. At Ibadan, there is a good relationship between leaf area eaten and the total number of microarthropods — mainly mites and Collembola — in the litter bags. The abundance of microarthropods depended on the moisture conditions. Hence, during the wet season the leaf tissues were consumed very rapidly by the fauna in about 5 weeks; during the dry season this process presumably stopped owing to their absence. The fauna thus migrated freely into the litter when it was moist. NYE (1961) attributed the rapid rate of litter disappearance in Ghana to the presence of great numbers of termites and ants, but at Ibadan these insects only account for 0.02 % of the total arthropod population.

5.3. Influence of earthworms on litter disappearance

In temperate regions lumbricids play an important part in burying fallen leaves. EDWARDS and HEATH (1963) found that leaf material disappeared three times faster from bags to which earthworms had access than it did from bags from which they were excluded. RAW (1962) estimated that earthworms buried over 90 % of the leaf litter from apple orchards. *Hyperiodrilus africanus* shows no such behaviour. However, BATES (1960) and BATES and BAKER (1960) showed that casts of an allied species, like many other earthworm casts, had a higher plant residue, and also a higher C, N and P content than the soil profile underneath, so presumably these earthworms utilize the leaf material fragmented by the soil fauna.

EVANS (1948) estimated that grassland in England contained 100—400 thousand earthworms per acre, weighing 350—500 lbs., and deposited 11 tons of earthworm casts per year. EVANS and GUILD (1947; from various authors) estimated that between 2.3—8.1 tons of wormcasts were produced per acre in mixed woodland soils each year. In the tropical forest at Ibadan, it was estimated that during the wet season (one collection only) there were about 140,000 earthworms per acre (57,000/ha.), weighing under 100 lbs., two-thirds of them being under 4 cm. in length. The earthworms deposited 90 tons of surface soil per acre per year (36 tonnes/ha.). Hence, *L. terrestris* produces about 1/3 oz. (9 g/m.) of wormcasts per year and *H. africanus* about 2.2 oz. (62 g/m.) per year. These estimates are fairly similar to the production of wormcasts by *H. africanus* on grassland at Ibadan, but more earthworms were collected (MADGE, in litt.).

6. Summary

This work investigates leaf-fall and litter disappearance in a tropical forest at Ibadan, Nigeria. Leaves fell throughout the year, but mainly during the dry season, when different tree species shed their leaves at different intervals. The annual rate of litter disappearance was high compared with temperate regions. Litter disappeared mainly during the wet season, owing largely to the activity of mites and Collembola. Numerous vertical earthworm casts were produced during the wet season, by *Hyperiodrilus africanus* (BEDDARD). These earthworms do not appear to consume the litter, unlike other earthworms in temperate regions.

6. Zusammenfassung

In dieser Arbeit wird der Blattfall und der Streuschwund in einem tropischen Forst bei Ibadan, Nigeria, untersucht. Die Blätter fallen das ganze Jahr über, aber hauptsächlich während der Trockenperiode, wenn verschiedene Baumarten ihre Blätter nach verschiedenen Intervallen abwerfen. Die jährliche Rate des Rotteschwundes war im Vergleich zu jener gemäßigter Gebiete hoch. Die Streu schwindet hauptsächlich in der Regenzeit, was großteils von der Aktivität von Milben und Collembolen herrührt. Zahlreiche vertikale Regenwurmlosung wurde durch *Hyperiodrilus africanus* (BEDDARD) während der Regenzeit produziert. Diese Regenwürmer scheinen im Gegensatz zu anderen Regenwürmern gemäßigter Gebiete keine Streu zu verzehren.

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